EFFECTS OF MARINE-DERIVED NUTRIENTS ON POPULATION DYNAMICS OF SOCKEYE SALMON (*Oncorhynchus nerka*)

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Abstract

The effects of marine-derived nutrients (MDN) on the productivity of sockeye salmon (*Oncorhynchus nerka*) stocks in Alaska were examined through nitrogen stable isotope analysis of smolts and mathematical models of the sockeye stock-recruit relationship. Smolt $\delta^{15}N$ was used to infer the degree to which smolts depend on MDN for their growth. We attempted to identify the characteristics of sockeye nursery lakes and watersheds that affect the availability of MDN to juvenile sockeye using multiple regression. Stock-recruit models incorporating MDN effects were fit to sockeye escapement-return data to test if fluctuations in sockeye stock productivity could be explained by changes in MDN input into nursery lakes. The magnitude of escapement and water residence time were the most important factors affecting the MDN availability to juvenile salmon. Mixing state of lakes and the distance from the coast were also found to significantly affect the MDN availability. We found that regional environmental fluctuations had a large effect on stock productivities in stock-recruit modeling. However, we did not find strong evidence to support our hypothesis that increases in MDN input to nursery lakes will result in increased productivity of sockeye stocks. Stock-recruitment data may be poorly suited to detection of the influence of MDN.

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General Introduction

From late spring through summer, sockeye salmon (*Oncorhynchus nerka*) begin their upstream spawning migration. Sockeye is the third most abundant species among Pacific salmon (Burgner 1991). In Bristol Bay, Alaska, the largest producer of sockeye salmon in the world, an average of 12.4 million sockeye has returned to spawn annually for the past five years (Alaska Department of Fish and Game 2006). This large number of salmon transports significant amount of nutrients to freshwater environments. In lakes with large spawning populations, the nutrients salmon bring in, which are referred to as marine-derived nutrients (MDN), have been estimated to constitute a significant portion of lake nutrient budget (Donaldson 1966; Finney 1998).

Spawning takes place from late summer through winter. The following spring, fry emerge from the gravel and immediately migrate to lakes associated with their natal streams. This use of lakes as their nursery is a characteristic of sockeye salmon that distinguishes them from other species of Pacific salmon, that spend their early life stage in streams or estuaries. Juvenile sockeye remain in their lake nurseries for the next one to three years, feeding mainly on limnetic zooplankton, before migrating to the ocean (Burgner 1991).

Many of the sockeye nursery lakes in Alaska are classified as oligotrophic. Past studies have shown that growth of juvenile sockeye is limited by the forage base in their nursery lakes (Koenings and Burkett 1987; Kline 1991). Past studies have also shown that marine mortality of sockeye is highest right after their ocean entry (Healey 1982; Bax 1983; Fisher and Pearcy 1988), and that early marine survival is related to the size at

ocean entry (Pearcy 1992; Koenings et al. 1993). Therefore, the nutrients released from salmon carcasses could result in increases in the size of smolts, and lead to higher survival of young salmon and subsequent increases in salmon production.

There were two objectives for my study. First, I attempted to identify the characteristics of sockeye nursery lakes and watersheds that affect the availability and relative importance of MDN to the growth of juvenile sockeye compared to nutrients from terrestrial sources, using the nitrogen stable isotope composition of sockeye smolts as an indicator of the MDN contribution to their growth. Second, I examined whether the addition of MDN to nursery lakes results in increased productivity of sockeye stocks, using stock-recruit models and sockeye escapement and return data.

Chapter 1

Effects of marine-derived nutrients on population dynamics of sockeye salmon (*Oncorhynchus nerka*)

Abstract

The effects of marine-derived nutrients (MDN) on the productivity of sockeye salmon (*Oncorhynchus nerka*) stocks in Alaska were examined through nitrogen stable isotope analysis of smolts and mathematical models of the sockeye stock-recruit relationship. Smolt $\delta^{15}N$ was used to infer the degree to which smolts depend on MDN for their growth. We attempted to identify the characteristics of sockeye nursery lakes and watersheds that affect the availability of MDN to juvenile sockeye using multiple regression. Stock-recruit models incorporating MDN effects were fit to sockeye escapement-return data to test if fluctuations in sockeye stock productivity could be explained by changes in MDN input into nursery lakes. The magnitude of escapement and water residence time were the most important factors affecting the MDN availability to juvenile salmon. Mixing state of lakes and the distance from the coast were also found to significantly affect the MDN availability. We found that regional environmental fluctuations had a large effect on stock productivities in stock-recruit modeling. However, we did not find strong evidence to support our hypothesis that increases in MDN input to nursery lakes will result in increased productivity of sockeye stocks. Stock-recruitment data may be poorly suited to detection of the influence of MDN.

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Introduction

A distinguishing characteristic of sockeye salmon (*Oncorhynchus nerka*), among other species of Pacific salmon, is their extensive use of lake rearing habitat during the juvenile stage of their life history. After emerging from the gravel, sockeye fry typically migrate to lakes associated with their natal stream habitats, where they exhibit a pelagic life style, feeding mainly on limnetic zooplankton for one to three years before seaward migration (Burgner 1991). The biological productivity in sockeye nursery lake habitat is important for the survival and growth of juvenile sockeye salmon. Although sockeye salmon acquire 99% of their body weight in the ocean, survival in the freshwater stage is much lower (about 1%) than ocean survival (about 10%) (Foerster 1968). In addition, most marine mortality occurs soon after entering the ocean (Healey 1982; Bax 1983; Fisher and Pearcy 1988), and is inversely related to size attained in freshwater (Pearcy 1992; Koenings et al. 1993).

Spawning adult salmon returning to their natal freshwater habitats bring in large quantities of nutrients annually in the form of their body mass (Kline et al. 1993; Bilby et al. 1996; Schmidt et al. 1998). For example, one million sockeye transport an estimated 64 100 $kg \cdot yr^{-1}$ of nitrogen to Karluk Lake, Kodiak, Alaska, while 43 200 $kg \cdot yr^{-1}$ and 800 $kg \cdot yr^{-1}$ are supplied by the other main nitrogen sources, rivers and rain, respectively (Finney 1998). Many of the lakes in Alaska used as the nursery by sockeye salmon are classified as oligotrophic, where nutrients limit primary production. In such systems, the nutrients supplied by salmon might be very important in maintaining the productivity of the lake.

Nitrogen derived from adult salmon is enriched in ^{15}N relative to nitrogen from other terrestrial sources. The $\delta^{15}N$ of adult sockeye averages about 11 to 12, while terrestrial sources of nitrogen have $\delta^{15}N$ values closer to zero (Kline et al. 1993; Welch and Parsons 1993; Satterfield and Finney 2002). This large difference in $\delta^{15}N$ makes it possible to trace and quantify marine-derived nutrients (MDN) in freshwater systems (Kline et al. 1990). The $\delta^{15}N$ value of sockeye smolts has been shown to have a strong positive correlation with the number of adult sockeye spawning in the system, and can be used to estimate the relative importance of MDN in the growth of juveniles (Kline et al. 1993; Finney 2000).

It has been postulated that declines of some sockeye stocks may be partly due to reduced nutrient loading because of low escapement (Finney et al. 2000; Stockner et al. 2000). In many lakes, the input of marine-derived nutrients was much higher prior to the advent of commercial fisheries. A reduction in marine-derived nutrients has been advanced as a possible explanation for reduced sockeye returns to some formerly highly productive systems, such as Karluk Lake (Schmidt et al. 1998; Finney et al. 2000).

The objectives of this study were to assess whether characteristics of sockeye nursery lakes could affect the availability of MDN to juvenile sockeye, and thus mediate the effects of MDN on stock productivity. The importance of MDN in the growth of juvenile salmon depends on the abundance of such nutrients in the system relative to the nutrients derived from terrestrial sources. The quantity of nutrients exported from watersheds into lakes rises with increasing watershed area (Kalff 2002). Lakes with large watershed areas are more likely to experience large inputs of terrestrial nutrients relative

to the nutrients derived from spawning salmon. In such lakes, MDN should be of secondary importance to the productivity of the system and to the growth of juvenile salmon. Because the stable isotope signature of terrestrial nitrogen is much lighter than that of nitrogen derived from adult salmon, juvenile salmon rearing in a lake in which nutrients from terrestrial sources are abundant would have a low $\delta^{15}N$ value.

Productivity of lake ecosystems can be limited by factors other than nutrients such as the availability of light for photosynthesis by phytoplankton. Because of limited light availability, the productivity of glacial lakes with high concentrations of suspended silt may not respond to increased nutrient input. Under such conditions, increased spawner abundance might not result in as large of a productivity increase of the lake. This would also be reflected in the nitrogen stable isotope signature of the juvenile salmon rearing in such lakes. Because phytoplankton preferentially assimilates the lighter isotope of nitrogen, ^{14}N, over the heavier ^{15}N, the nitrogen isotope signature of phytoplankton, and of all organisms whose lives depend on the primary production of the lake, will be lighter than that of the source nitrogen if there is an excess of nitrogen in the environment. Thus, juvenile salmon in glacial lakes might be expected to benefit less from the addition of MDN compared to their counterpart in non-glacial lakes.

Salmon typically cease feeding before entering their natal streams and depend entirely on their body energy reserves for migration, maturation of gonads, and spawning. In addition to the intense physical activity of the migration, the physical, chemical, and physiological changes they must undergo during migration extensively deplete their body reserves of fat and protein (Burgner 1991). In one study, male and female sockeye

salmon on average had lost 42% and 61% of body protein respectively, through migration and spawning (Idler and Clemens 1959). It is possible that the salmon that travel long distances to their spawning grounds lose more body protein than the ones who travel shorter distances during migrations. Therefore, we examined whether the distance from the coast to the mouth of a particular nursery lake affects the availability of MDN to the growth of juvenile sockeye.

Stratification of the water column in lakes limits exchange of materials, including nutrients, between layers of water within the lake. Most temperate lakes stratify during summer months because of a density gradient in the water column created by solar energy input to the lake surface. As the lake water is cooled at the surface in fall the density gradient in the water column diminishes to the point at which wind is able to mix the entire water column. Mixing of the water column refurnishes the euphotic zone with nutrients from the hypolimnion, allowing nutrients to be recycled within the lake. Incomplete mixing of the water column (meromixis) limits nutrient supply to the epilimnion by reducing nutrient recycling and affects primary production. Three of the lakes included in this study (Coghill, Hugh Smith, and Redoubt) are known to have a persistent stratified state with a dense, anoxic layer of saline water, which does not mix with the surface layer above (Edmundson et al. 1992; Geiger et al. 2003; Geiger 2003). It is likely that some nutrients entering these lakes are trapped in the bottom layer, and thus do not contribute to the productivity of the lake.

We analyzed nitrogen stable isotope of smolts from 21 Alaska lakes, comparing it to both spawner abundance and lake characteristics that might affect the importance of

MDN in salmon growth. We also examined the effect of spawner abundance and lake characteristics on the productivity of 16 Alaska sockeye stocks, as reflected in the relationship between spawning adults and the number of adult offspring they produce. We tried to quantify the effects of MDN by first fitting mathematical models to historical escapement and return data, then examining our estimates to see if the magnitude of the effect differed for various lake types.

Materials and Methods

Study Sites

Twenty-three sockeye stocks and associated nursery lakes in Alaska were included in this study (Table 1). Particular stocks of sockeye salmon (and their nursery lakes) were chosen based on the availability of smolt samples, escapement and return data, and lake morphometric data. The morphometric data (lake surface area, mean depth and/or lake volume) for the nursery lakes were obtained from literature and ADF&G reports. The distances from the coasts to the outlets of the study lakes were measured on digital spatial data obtained from National Hydrography Dataset (USGS 2004a). The study sites encompassed a large geographic area (130.67°W – 161.02°W, 55.10°N – 61.10°N) with climatic differences. Because sockeye stocks in the same geographic region have been shown to exhibit a similar pattern in their productivity (Peterman et al. 1998), the stocks in this study were grouped by five geographic regions; Alaska Peninsula (AKP), Bristol Bay (BB), Kodiak (KOD), Cook Inlet/Prince William Sound (CI/PWS), and Southeast (SE) for the purpose of population modeling. The study lakes

varied in size, with surface area ranging from 0.9 to 2 642 km^2 and volume ranging from 5.1 x 10^6 to 115 310 x 10^6 m^3. The volumes of the three meromictic (incomplete mixing of water column) lakes included in this study (Coghill, Hugh Smith, and Redoubt) were based on the depths of the top mixed layer because there is no exchange of water and materials between the top and bottom layers in these lakes as discussed earlier.

Watershed Area and Annual Discharge

The watershed areas of the nursery lakes were estimated based on the National Elevation Dataset (NED; resolution 2 arc second) obtained from the National Center for Earth Resources Observations and Science (EROS; 2004), using the Watershed function in ArcGIS (version 9.0) spatial analyst tools.

We estimated the annual discharge from the nursery lakes using stream flow data obtained from the US Geological Survey Water Resources website (USGS 2004b). The annual mean flow values between 1910 and 2002 were averaged for each of 382 gauging stations in Alaska. The averaged flow values were divided by the drainage area for each gauging station to express the annual flow on a per unit drainage area basis ($m^3 \cdot year^{-1} \cdot km^{-2}$). Where direct flow measurements were not available, the values of annual flow/drainage area at the outlet of the nursery lakes were interpolated from the measured values at the nearest 15 gauging stations by inverse distance weighted interpolation using an ArcGIS geospatial analyst tool with a power value of 2. These values were then multiplied by the drainage area of each lake to estimate annual discharge ($m^3 \cdot year^{-1}$). The water residence time (year) of the nursery lake was obtained by dividing the lake volume

by the estimated annual discharge.

Escapement and Return Data

Sockeye escapement and brood year total return data for 16 sockeye stocks were obtained from the Alaska Department of Fish and Game (ADF&G), Division of Commercial Fisheries regional offices, and from ADF&G publications.

Two lakes in Southeast region (Chilkat and Speel) have been stocked with sockeye fry in the past. For the purpose of modeling stock-recruit relationships, the number of spawners equivalent to the number of fry released was calculated by dividing the number of fry by the egg-to-fry survival rate (0.127; Quinn 2004) and by fecundity (3654), then added to the escapement of the corresponding years.

Analysis of Smolt Stable Isotope Data

Seven hundred and sixty-three sockeye smolts collected from 21 sockeye producing systems in Alaska were analyzed for nitrogen stable isotope composition (Table 2). Smolts from Southeast region were analyzed by David Barto of ADF&G (Barto 2004). The number of smolt samples from a particular system and year ranged from five to 68. Muscle tissues from smolt samples were removed with a scalpel and either oven- or freeze-dried and then homogenized. Nitrogen stable isotope compositions were analyzed using a continuous-flow isotope ratio mass spectrometer (Europa Scientific 20/20 or ThermoFinnigan Delta+), and expressed in conventional $\delta^{15}N$ notation (Satterfield and Finney 2002).

The effects of characteristics of sockeye nursery lakes (watershed area, glacial coverage in the watershed, distance from the coast, and permanent stratification) on the availability of MDN to juvenile salmon were examined by multiple linear regression, using the lake characteristics as explanatory variables and the mean of observed smolt $\delta^{15}N$ for each lake and year as a response variable. The multiple regression model was fitted to the data by weighted least squares using the number of observations in each lake and year as the weights. The multiple regression model was formulated as follows:

$$(1) \qquad \delta^{15} N_{smolt,i,t} = \alpha + \beta_1 \left(\frac{\text{MDN input}}{\text{lake volume}} \right)_{i,t-1} + \beta_2 \left(\frac{\text{watershed area}}{\text{lake volume}} \right)_i + \beta_3 \left(\frac{\text{glacier coverage}}{\text{watershed area}} \right)_i + \beta_4 (\text{distance traveled})_i + \beta_5 (\text{mixing})_i$$

where i = stock/drainage

t = brood year

"MDN input" in the regression equation was calculated as

$$(2) \qquad \text{MDN input}_{i,t} = \sum_j S_{i,t-j} e^{(-(j+0.5)/RT_i)}$$

where S_i = salmon escapement in lake i, RT_i = water residence time of lake i, and j is the number of years before year t. The effects of MDN are expected to persist over several years from the time the nutrients are introduced as the carcasses of spawning adults because of retention of nutrients in the system. Over time, nutrients are lost from the system, and the effects of MDN on the productivity of the system are also expected to diminish. We assumed that the amount of nutrients brought in by salmon is proportional to the escapement. We also assumed the amount of nutrients retained in the system was

proportional to the amount of water retained in the lake annually. Because our assumption was that nutrients were exported from a lake with out-flowing water, the nutrients derived from the carcasses of spawning salmon would be continuously lost from the system before the nutrients can be utilized by newly emerged fry next spring. To account for this loss of nutrients, a half (0.5) year was added to the number of years passed since the spawning (j). To avoid an abrupt increase in MDN input at the beginning of the recorded escapement data, we used the value of average escapement in the 100 years previous to the beginning of the escapement record, and then calculated MDN input.

One of the lakes in this study, Chignik Lake, was a special case in the sense that another nursery lake with a distinct spawning stock, Black Lake, is located upstream. Therefore, Chignik Lake receives the water from upstream Black Lake. Because Black Lake has a spawning stock distinct from that of Chignik Lake, and the fish of the Black stock spawn and die upstream of Chignik Lake, the Chignik stock was expected to receive the benefit of MDN not only from the spawning fish of its own stock, but also from those of the Black stock as well. To reflect this additional MDN input from the upstream spawning stock, the MDN exported from Black Lake was modeled as the MDN input into Black Lake less the MDN retained in Black Lake (Eq. 3), and this quantity was added to the number of spawners in Eq. 2 for Chignik Lake.

(3) $$\text{MDN Export}_{\text{Black,t}} = S_{Black,t} + \sum_{j-1} S_{Black,t-j-1} e^{\left(-(j+0.5)/RT_i\right)} - \sum_{j} S_{Black,t-j} e^{\left(-(j+0.5)/RT_i\right)}$$

To account for the size of lakes to which nutrients are imported, MDN input and watershed area were divided by the lake volume. The ratio of watershed area

covered by glaciers was used to assess the influence of glaciers to the lake ecosystem. The term "mixing" in the regression equation is a dummy variable (meromictic = 0, holomictic, or complete mixing = 1).

All independent variables except the categorical variable ("mixing") were standardized by dividing by the maximum value for each variable to eliminate the effect of scale on the regression and to make the coefficients roughly comparable to one another. The significance of each regression coefficient was tested using t-tests. The significance of each term in the regression was further examined by backward stepwise model selection, using the Akaike Information Criterion corrected for small sample size (AIC_C) to determine whether explanatory variables should be retained. The AIC_c was calculated as:

$$(4) \qquad AIC_C = n\ln(RSS) + \frac{2np}{n-p-1}$$

where RSS is the residual sum of squares from model fitting, n is the number of observations, and p is the number of parameters included in the model.

Stock-Recruit Models

To test the effect of MDN on the productivity of sockeye salmon stocks in Alaska, we fit several stock-recruit models to available sockeye escapement-total return data. We assumed density-dependent compensation in the stock-recruit relationship, and used the classic Ricker model (Eq. 5) as a basis of model development.

$$(5) \qquad \ln\frac{R_{i,t}}{S_{i,t}} = \ln(\alpha_i) - \frac{S_{i,t}}{\beta_i} + \varepsilon_{i,t}$$

The $S_{i,t}$ and $R_{i,t}$ denotes sockeye escapement and return, respectively, for stock i in brood year t, α_i is the intrinsic productivity parameter for stock i, β_i is a parameter that determines the carrying capacity for stock i, and $\varepsilon_{i,t}$ is normally distributed random error for stock i in year t.

We modified the Ricker stock-recruit model (Eq. 5) to include the effect of MDN from the carcasses of spawning salmon on future salmon production. For parsimony, and because it had the largest effect in analyses of smolt isotope data, the only lake characteristic considered in this analysis was an effect of water residence time on MDN input. The MDN input to the lake was modeled as in Eq. 2 – 3, and incorporated in stock-recruit models as in Eq. 6 – 8.

$$(6) \qquad \ln\frac{R_{i,t}}{S_{i,t}} = \ln(\alpha_{i,t}) - \frac{S_{i,t}}{\beta_{i,t}} + \varepsilon_{i,t}$$

$$(7) \qquad \alpha_{i,t} = \overline{\alpha}_i + k_{i,\alpha}\sum_j S_{i,t-j}e^{(-(j+0.5)/RT_i)}$$

$$(8) \qquad \beta_{i,t} = \overline{\beta}_i + k_{i,\beta}\sum_j S_{i,t-j}e^{(-(j+0.5)/RT_i)}$$

In this model (Eq. 6 – 8), the productivity of the stock ($\alpha_{i,t}$) and the carrying capacity ($\beta_{i,t}$) are formulated to have two parts: the baseline values ($\overline{\alpha}_i$, $\overline{\beta}_i$) and the effect of MDN ($k_i\sum_j S_{i,t-j}e^{(-(j+0.5)/RT_i)}$) additive to these baseline values. The effect of MDN is modeled to be proportional to the amount of MDN retained in the nursery lake. The factors

$k_{i,\alpha}$ and $k_{i,\beta}$, scale the effect the retained MDN have relative to the baseline productivity and carrying capacity. Accordingly, this model form will be referred to as "the $k_{\alpha,\beta}$ model." The $k_{i,\alpha}$, and $k_{i,\beta}$ were constrained to be positive.

We also considered models in which MDN only affects either the intrinsic productivity of the stock ($\alpha_{i,t}$; Eq. 9; referred to as "the k_{α} model"), or the carrying capacity ($\beta_{i,t}$; Eq. 10; referred to as "the k_{β} model").

$$\ln\frac{R_{i,t}}{S_{i,t}} = \ln(\alpha_{i,t}) - \frac{S_{i,t}}{\overline{\beta}_i} + \varepsilon_{i,t} \tag{9}$$

$$\ln\frac{R_{i,t}}{S_{i,t}} = \ln(\overline{\alpha}_i) - \frac{S_{i,t}}{\beta_{i,t}} + \varepsilon_{i,t} \tag{10}$$

For all the model forms above, we also examined the effects of climate on the spawner-recruit relationship by including additional parameters (Eq. 11). Previous studies have shown that climate has a profound effect on the stock-recruitment relationship in many sockeye salmon stocks (Hare and Francis 1995; Beamish and Bouillon 1993; Adkison et al. 1996). Climatic influences are large enough that they should be included in any model of a long time series of stock and recruitment data. Unfortunately, such climate-related increases in productivity often result in increases in escapement (Bocking and Peterman 1988). This might hinder separation of the effect of climate and the effect brought about by MDN input. We attempted to separate the effect of climate from the MDN effect by considering several stocks in close proximity simultaneously. Climate-induced changes are usually similar for stocks in the same region (Peterman et al. 1998). Therefore, it should be possible to distinguish a shared,

climate-driven pattern from localized fluctuations in recruitment, including those due to MDN. Accordingly, the effect of climate was modeled as

$$(11) \qquad \ln\frac{R_{i,t}}{S_{i,t}} = \ln(\alpha_{i,t}) - \frac{S_{i,t}}{\beta_{i,t}} + c_i E_{r,t} + \varepsilon_{i,t}$$

where $E_{r,t}$ was an environmental influence that affects all stocks in a region r in the same fashion; the magnitude can vary from stock to stock, according to the stock-specific parameter c_i. Models including the parameters c_i and $E_{r,t}$ will be referred to as "the *cE* model." The environmental effect $E_{r,t}$ was estimated for all years for which stock-recruit data were available for more than one stock within a region. To ensure a consistent climatic effect among stocks in a region, the parameters c_i were constrained to be positive. The sum of the estimates of E was constrained to zero for each region, so that $c_i E_{r,t}$ and $\alpha_{i,t}$ would not be confounded.

Parameter Estimation and Model Selection

Model parameters were estimated using a maximum likelihood method, by fitting the models to the sockeye escapement and total return data. The models were fitted to all stocks in the same region simultaneously. The corrected Akaike Information Criterion (AIC_C) was used to select the model forms that best explained the variability in the escapement-return data for each region. The AIC_C was calculated using Eq. 4.

Calculation of MDN Effects on the Stock-Recruit Relationship

To assess the magnitude of the influence of MDN on the productivity of sockeye

stocks, we calculated indices of the influence of MDN on productivity (I_α) and carrying capacity (I_β) for each stock based on estimated parameters as follows:

$$(12) \qquad I_{\alpha,i} = \frac{k_{i,\alpha} \sum_j S_{i,t-j} e^{(-(j+0.5)/RT_i)}}{\overline{\alpha} + k_{i,\alpha} \sum_j S_{i,t-j} e^{(-(j+0.5)/RT_i)}}$$

$$(13) \qquad I_{\beta,i} = \frac{k_{i,\beta} \sum_j S_{i,t-j} e^{(-(j+0.5)/RT_i)}}{\overline{\beta} + k_{i,\beta} \sum_j S_{i,t-j} e^{(-(j+0.5)/RT_i)}}$$

The indices I_α and I_β represent the proportion of the overall productivity and carrying capacity, respectively, due to MDN. The I_α and I_β were calculated for each brood year, then averaged for each stock.

We calculated stock-recruit relationships for the stocks found to have a significant MDN effect. Because of the cumulative effect of past escapement, the intrinsic productivity (α) and the carrying capacity (β) parameters of our MDN models (the k_α, k_β, and $k_{\alpha,\beta}$ models) will change from one year to the next. To predict the equilibrium recruitment for a particular level of escapement, the selected model was projected 100 years with escapement held constant. To calculate the stock-recruit relationship with the MDN effect, this projection was repeated for 100 different levels of escapement between zero and the highest historical escapement for each stock.

Results

Watershed Area and Residence Time

Watershed areas and residence time of the study lakes are summarized in Table 1.

Three of the study lakes (Iliamna, Karluk, Spiridon) had USGS gauging stations located at the outlets, and for these, direct measurements were used for the calculation of the residence time.

Analysis of Smolt Stable Isotope Data

The regression coefficients, standard errors, and p-values are presented in Table 3. In conformance with our hypothesized mechanisms, the estimated coefficient for MDN·lake volume^{-1} (β_1) was positive, while the coefficients for watershed area·lake volume^{-1} (β_2), glacier·watershed area^{-1} (β_3), distance traveled (β_4) were all negative.

Also in conformance with expectations, the coefficient for mixing (β_5) predicted that the smolt $\delta^{15}N$ would be 1.804 per mil higher in holomictic lakes than in meromictic lakes, given the same level of MDN, watershed area, glacier coverage, and distance from the coast. At $\alpha = 0.05$, MDN input, distance traveled, and mixing state were significant. The adjusted R^2 of the model fit was 0.61.

The amount of MDN input had by far the largest estimated effect on smolt $\delta^{15}N$ ($\beta_1 = 7.41$). Among the lake characteristics examined, the distance from the coast affected the smolt $\delta^{15}N$ most ($\beta_4 = -2.41$). The mixing state of the lake had the third largest effect ($\beta_5 = 1.80$).

The backward stepwise model selection based on AICc retained MDN input, distance traveled, and mixing state of the lake. The regression coefficients, standard errors, and p-values were very similar to those from the full model (Table 4). The adjusted R^2 for the reduced model was 0.63 (Table 5).

Population Models

The classic Ricker model (i.e., density-dependent compensation) explained about half of the variation in the productivity of Alaska Peninsula and Southeast stocks, and about a quarter of the variation in the productivity of Kodiak and Cook Inlet/Prince William Sound stocks (Table 6). This model explained < 1% of the variation in the productivity of Bristol Bay stocks.

The inclusion of an environmental term ($E_{r,t}$) common to all stocks in the same region explained a large amount of variation in the productivity of the sockeye stocks. The additional explained variation ranged from 24.5% to 67.2% among regions (Table 7). Especially notable were the Bristol Bay stocks, where the variation explained by the model increased from < 0.1% to 66.7% for the Egegik stock, < 0.1% to 34.7% for the Kvichak stock, and 1.7% to 90.2% for the Ugashik stock. Despite explaining such large portions of the variation in recruitment, including the environmental effect reduced model performance (resulted in higher AIC_C) compared to models without the environmental effect (Table 6, 7, 8, 9) because of the large number of parameters estimated.

The estimates of the influence of climate (c_i) were comparable among stocks in the same region, except for the Southeast stocks (Table 7, 9). This suggests that the productivity of the stocks in the Alaska Peninsula, Bristol Bay, Kodiak, and Cook Inlet/Prince William Sound regions indeed have responded to some common environmental factor. In the Southeast region, only one stock (Chilkoot) had a large enough c_i for the estimated environmental effect to make any change in model fit (Table 7); the resultant estimates of the environmental factor (E_i) were thus stock-specific and

not useful for separating environmental fluctuations from the influence of MDN.

Including the effect of MDN ($k_{i,\alpha}$ and $k_{i,\beta}$) in addition to the density-dependent compensation in the model resulted in only small increases in the variation explained by the model, except for the Southeast stocks for which an additional 14% of the variation was explained (Table 6, 8). When compared to the classic Ricker model, the inclusion of the MDN terms did not significantly improve the model in any region (Table 6). When the model with MDN effects (Table 8) was compared to model with environmental effects (Table 7), it performed more poorly (higher AIC_C) for the Bristol Bay stocks and Kodiak stocks, despite large differences in the number of parameters estimated. MDN effects also did not explain much more of the variation in recruitment when added to the model that included environmental effects (Table 7, 9), except, again, for the Southeast stocks.

We calculated the proportion of the intrinsic productivity and the carrying capacity attributed to MDN (I_α and I_β) from the estimated parameters for the $k_{\alpha,\beta}$ model with climatic effects, irrespective of whether they were found significant based on our AICc criterion. These proportions ranged from < 0.1% to, in some extreme cases, nearly 100% (Table 10). For most of the stocks, the effect of MDN was restricted to their carrying capacity β, while only two of the stocks (Karluk, Chilkoot) showed some sign of an MDN effect on intrinsic productivity α. The influence of MDN were estimated to be especially large for the Chilkoot (on intrinsic productivity, α), Black, Ugashik, Eshamy, Chilkat, and Speel (on carrying capacity, β) stocks. No strong relationship was found between the magnitude of MDN influence and any of the lake and watershed

characteristics examined. Contrary to our original hypothesis, among the lakes that showed strong MDN influences were two of the fastest flushing lakes in this study, Black (residence time: 0.058 years) and Speel (residence time: 0.075 years).

Except for the $k_{\alpha,\beta}$ models in the Bristol Bay and Kodiak regions, environmental effects were never significant. However, the purpose of including these effects in our model was to eliminate the possible confounding of climate-driven changes in productivity (e.g., favorable climate results in increased escapements and productivity) from the effects of MDN. For this reason, we more closely examined the two best-supported models for each region that included climatic effects. Among the models selected (Table 11) were: the k_{β} and the $k_{\alpha,\beta}$ models for the Black stock (Alaska Peninsula), the k_{β} model for the Ugashik stock (Bristol Bay), the k_{α} model for the Karluk stock (Kodiak), the k_{β} model for the Eshamy stock (Prince Williams Sound), and the k_{β} and the $k_{\alpha,\beta}$ models for the Speel stock (Southeast). The models selected roughly corresponded to those where the largest estimated proportions of the intrinsic productivity and carrying capacity were attributed to MDN (Table 10).

The equilibrium stock-recruit relationships for these models are shown in Fig. 1 – 5, along with the stock-recruit relationship based on the climate-influenced Ricker model (the cE model) without the MDN effect. For the Black and Speel stocks, the k_{β} model returns were predicted to increase more rapidly and reach the maximum at lower levels of escapement than with the Ricker model (Fig. 1, 2). For these two stocks, the maximum sustainable yields (MSY) predicted by the k_{β} models were higher, and the escapements that produced the MSY (S_{MSY}) were lower than those predicted by the Ricker model

(Table 12). Carrying capacities (β) were lower than those predicted by the Ricker model.

The effects of MDN on the Karluk stock-recruitment relationship showed opposite changes to those estimated for the Black and Speel stocks (Fig. 3). At low escapement levels, the predicted returns from the k_α model were lower than those predicted from the Ricker model, but became higher at high levels of escapement. The MSY predicted by the k_α model was lower than that predicted by the Ricker model, but the carrying capacity predicted by the k_α model was higher than that predicted by the Ricker model (Table 12).

For the Ugashik and Eshamy stocks, the predicted returns from the k_β model were lower than those from the Ricker model at low levels of escapement (Fig. 4, 5). However, the carrying capacities for these two stocks continued to increase without reaching equilibrium at high spawner densities, and so did the predicted returns. Because of this, MSY were not calculated for these two stocks (Table 12).

Discussion

Smolt Isotope Analysis

The results of smolt nitrogen stable isotope analysis indicated that sockeye escapement and water residence time are the most important determinant of the availability of MDN to juvenile sockeye among the variables examined in this study, explaining 53% of the variance in smolt $\delta^{15}N$ value. The estimated coefficient for MDN input (β_1) of 7.41 implies that input of 3.97 adult sockeye per 10^3 m^3 of lake water (the maximum MDN input value in the dataset, recorded from Red Lake, Kodiak; Table 2)

would increase smolt $\delta^{15}N$ value by 7.41‰.

Although not explicit in the regression equation, the water residence time of a nursery lake also had a strong influence on the MDN availability to juvenile salmon. Because our assumption was that MDN imported to the system would be exported with the water leaving the system, we also expected a positive relationship between residence time and $\delta^{15}N$ of smolts. However, because residence time is related directly to lake volume (residence time = lake volume·lake discharge^{-1}), and indirectly to watershed area (lake discharge = watershed area x discharge estimate per unit watershed area), the relationship between residence time and the MDN availability was unclear. Furthermore, moderate to high correlations between residence time and other potential covariates made it necessary to exclude residence time as a covariate in the multiple regression analysis. Instead, the effect of residence time was included in the estimates of MDN input, influencing the persistence in the system of nutrients from past abundance of spawning adults as described in Eq. 2.

To assess the effects of residence time on MDN availability, we re-ran our regression analyses, substituting sockeye escapement a year previous to the smolt sampling for the "MDN input" variable in the regression equation; i.e., we did not account for nutrients from escapements more than one previous year, which should be important in lakes with long water residence times. While the original regression model explained 66% of variance in the data, the model with escapement limited to the previous year explained only 37% of variance. This result suggests that the water residence time of lakes positively affects MDN availability to juvenile salmon, and that our assumption

that hydrology affects the MDN contribution from previous years' spawners was reasonable.

Distance from the coast had the second largest effect on smolt $\delta^{15}N$. The estimated coefficient β_4 of -2.41 indicates that smolt $\delta^{15}N$ value decreased by 2.41‰ for a distance of 147km, the distance to the nursery lake located farthest from the point of freshwater entry among the lakes included in this study (Upper Russian Lake). This supported our assumption that, having ceased feeding upon entering freshwater, salmon would continually lose nutrients in their bodies through metabolic activity during their upriver migration. Therefore, the longer they have to migrate, the less MDN they bring into their spawning and nursery habitats for their offspring. However, there is another possible explanation for this relationship. Some sockeye spawn downstream of the primary nursery lake in the drainage, and the fry later migrate upstream to the lake where they rear. In such a case, the estimate of MDN based on escapement would overestimate the MDN input to the nursery lake. The Upper Russian Lake sockeye stock is likely an example of this factor. Most adults have been observed to spawn downstream of Upper Russian Lake, and this seem to be reflected in the relatively low $\delta^{15}N$ value in these smolts. The amount and use of suitable spawning habitat both downstream and upstream of nursery lakes needs to be considered when assessing the MDN input to the lake based on escapement, although this information is often lacking. Another potential confounding factor is differences in growth rates or age at return among systems, which might result in difference in body mass among stocks.

The third significant factor was whether lake water completely mixed; smolt $\delta^{15}N$

was estimated to be 1.80‰ higher in the holomictic lakes than in the meromictic lakes.

As expected, the estimated effect of watershed area per volume of lake (β_2) was negative, indicating that smolt $\delta^{15}N$ decreases with watershed area, a proxy for terrestrial input of nutrients. However, the small coefficient and large standard error made the estimate insignificant at $\alpha = 0.05$. A relatively small effect of watershed area on smolt $\delta^{15}N$ might mean that the nutrient export from watershed is not controlled by watershed area per se; biologic, climatologic and geologic processes within watersheds have a large influence on nutrient export through processes such as soil composition and precipitation, and these processes may vary significantly among watersheds.

As expected, the estimated effect of the fraction of the watershed covered by glaciers was negative, but the effect was also found to be statistically insignificant. This was most likely caused by the large variability in smolt $\delta^{15}N$ among watersheds with little glacial influence. Among the 21 lakes included in the multiple regression, 12 lakes do not have glaciers within their watersheds. Another six lakes have between 0.2% to 5% glacier coverage in their watersheds, while only three lakes (Chilkoot, Coghill, and Tustumena) have glacier coverage greater than 19% of watershed. While the smolt $\delta^{15}N$ content in the three lakes with high glacier coverage were invariably low (mean 9.03 ± 0.90 ‰), the smolt $\delta^{15}N$ for the rest of lakes were highly variable (mean 10.50 ± 4.74 ‰), although on average higher than those from the highly glaciated watersheds.

Population Models

Although the smolt isotope evidence suggests that MDN imported to freshwater

ecosystems by adult salmon are used by juvenile sockeye salmon, it is still not clear whether the addition of MDN to sockeye fry rearing habitats results in increased productivity of stocks. Our stock-recruit modeling suggested that the variation in stock productivity was driven mostly by the environment, rather than by MDN input to the sockeye nursery lakes. The exception to this was the Southeast stocks, for which the MDN input also explained a large portion of variation in the productivity. However, this might have been due to lack of a common pattern in the productivity among the Southeast stocks. Because the variation due to environmental factors was not properly accounted for, some of the variation in the productivity due to environmental factors could have been incorrectly attributed to the MDN effect. The converse could be true for the other regional groups. Due to the practical difficulties managers face in attaining a target escapement goal, favorable environmental conditions that lead to higher returns will often result in a high escapement (Bocking and Peterman 1988), and the benefits of the resultant MDN could be attributed to the environment. However, we found little evidence of MDN effects on the stock-recruitment relationships even when climatic effects were not included in the models.

The MDN effects were not estimated to be particularly important for the productivity of the stocks whose nursery lakes had characteristics that favor the transfer of nutrients from adult carcasses to juvenile salmon (Table 10). For example, smolt isotope analysis indicated that a long water residence time favors MDN transfer from adult to juvenile salmon. However, two of the stocks, Black and Speel, that showed particularly large effects of MDN on the carrying capacity parameter, use two of the

fastest flushing lakes among our study lakes for the nursery.

Model selection results suggest that the MDN effects in the stock-recruit relationship were significant for one of the stocks in each region (Table 11). Also, the proportions of the intrinsic productivity (α) and/or carrying capacity (β) attributed to MDN (Table 10) were large for the stocks with significant MDN terms (either k_α, k_β, or both). However, these models implied stock-recruitment relationships with counterintuitive management implications. For example, the models predicted a higher maximum yield and a higher maximum return for the Black stock and the Speel stock, respectively, compared to the prediction by the Ricker model (Table 12). However, these high yields and returns occurred at low escapement levels; the suggestion is that MDN effects imply lower escapement goals.

Including MDN terms resulted in an entirely different effect on the estimated stock-recruitment relationship for Ugashik and Eshamy stocks, as the predicted returns kept increasing with increasing escapement. Because regional environmental fluctuations explained so much variation in the data for these two stocks, there was very little variation in $\ln(R/S)$ left unexplained. As a consequence, the residuals show only a slight relationship to the number of spawners (Fig. 6, 7) except at very low levels of escapement. It is possible that compensatory density-dependence was masked by the environmental variation, leading to an inability to estimate the limits to recruitment.

In contrast, the plot of $\ln(R/S)$ against escapement for the Karluk stock (Fig. 8) shows large contrast even after the variation due to the regional environmental fluctuations is removed. This resulted in a more distinct slope, which translated to a

well-defined density-dependent compensation (Fig. 3). Additional variation in the productivity of the Karluk stock explained by including MDN effect was also small (1.9%). However, the AIC_C suggested that the k_α model for the Karluk stock explained the data as well as the Ricker model (Table 11).

Our models' inability to detect systematic influences of MDN on productivity could suggest that overall effects are minor and not felt in a systematic fashion. Alternatively, it may indicate that the way we chose to model MDN input to lakes did not accurately capture the mechanisms by which MDN is imported and retained in lakes. However, MDN input modeled the same way explained a large portion of variation in smolt $\delta^{15}N$, suggesting that our estimates of MDN input were reasonable.

Stock-recruitment data may be intrinsically ill suited for detecting the influence of marine-derived nutrients. Salmon carcasses would be expected to contribute the most nutrient in the year immediately following spawning. However, the effects of parents on survival of their own offspring are already included in conventional stock-recruit relationships; the effects of MDN can only be detected when they persist into subsequent years, where they would undoubtedly be weaker. MDN effects would be most distinguishable in slowly flushing lakes where historical spawner abundances included several multi-year periods of low escapements separated by multiple years of high escapements. In addition, numerous other factors influence whole life-cycle survival, which is highly variable in salmon. For all of these reasons, the power to detect even fairly strong effects of MDN in the stock-recruitment relationship may be low.

Conclusions

Our study showed that the nutrients released from carcasses of adult salmon are incorporated into lentic ecosystems of sockeye nursery lakes and make an important contribution to the nutrition of juvenile salmon. In addition, hydrological conditions of the nursery lakes such as water residence time, distance from the coast, and whether the water column mixes were found to affect the availability of MDN to juvenile salmon. Conditions under which salmon fry benefit most from MDN input from spawning sockeye are lakes with long water residence times, short distances from the coast, and where the water columns undergo complete mixing.

Watershed area and glacial coverage of watershed were not found to significantly affect the content of MDN in juvenile salmon, although the estimated effects were of the type expected. We speculate that the biology, geology and climate of watersheds complicate estimating terrestrial nutrient import into lakes based on watershed area.

Although there was strong evidence for MDN influences on sockeye smolt, and strong evidence that hydrological characteristics of nursery lakes affected the strength of this effect, in our stock-recruitment analyses we did not find much evidence to support our hypothesis that increases in MDN input to sockeye nursery lakes will result in increased productivity of sockeye stocks. The analysis of stock-recruit data for 16 Alaska sockeye stocks suggests that environmental conditions have a much larger influence on sockeye stock productivity than that of MDN. However, stock-recruitment data may be poorly suited to detecting the influence of MDN on productivity.

A more fruitful approach in estimating the effects of MDN on productivity might

be to more directly investigate the mechanisms by which MDN might improve stock productivity. The MDN concentration in smolts should be compared to smolt growth, age at emigration to the ocean, total biomass of smolt produced, and subsequent marine survival. Additional fruitful areas of research would be further investigations of the transfer of MDN through the limnetic ecosystem, and studies on how MDN are recycled and retained in sockeye nurseries, including watersheds and hyporheic zones.

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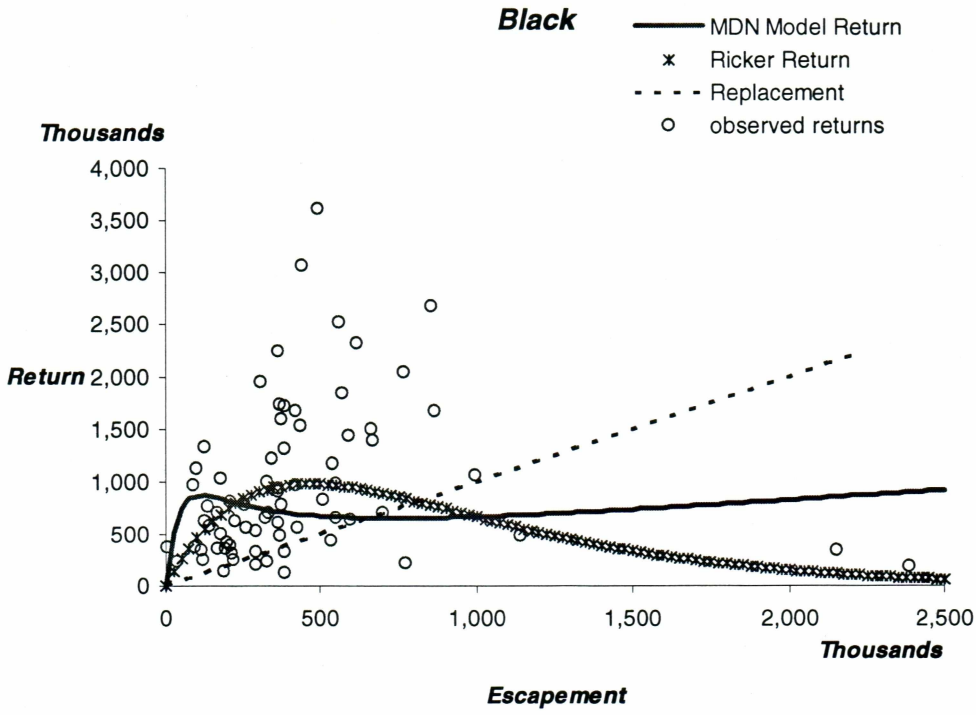

Fig. 1. Simulated stock-recruit relationships for the Black Lake stock using the model selected based on AIC_C.

Fig. 1 – 5. Simulated stock-recruit relationships using the model selected based on AIC_C for the Black, Speel, Karluk, Ugashik, and Eshamy stocks. The MDN models were run for 100 years at each escapement level using estimated parameters to obtain an equilibrium return (solid line). The *cE* model return (*) is also shown. Open circles are observed sockeye escapement-return data.

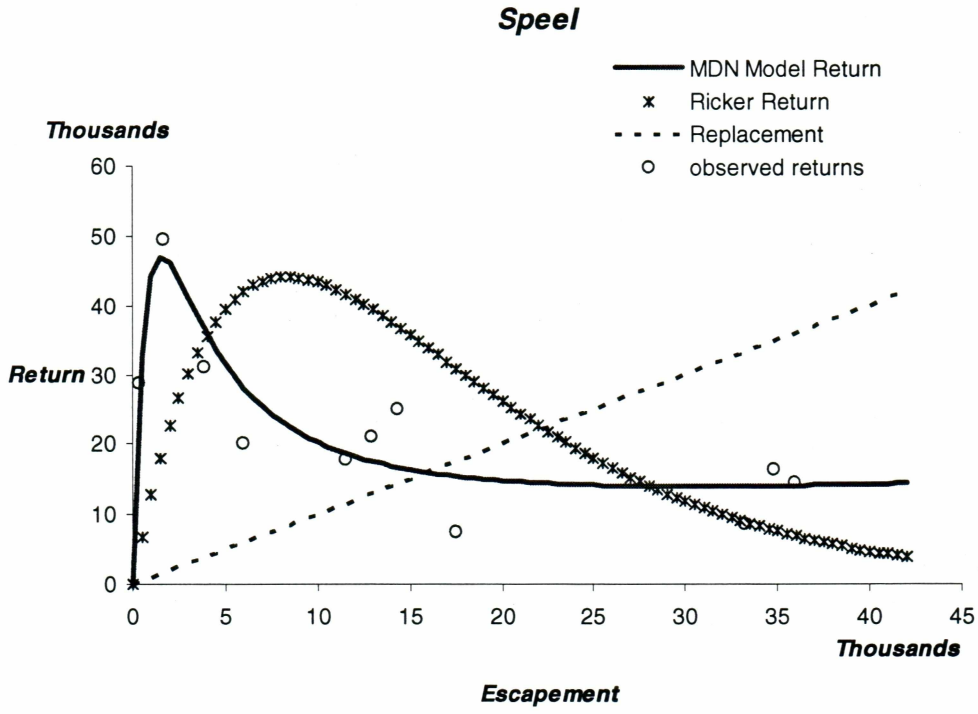

Fig. 2. Simulated stock-recruit relationships for the Speel stock using the model selected based on AIC_C.

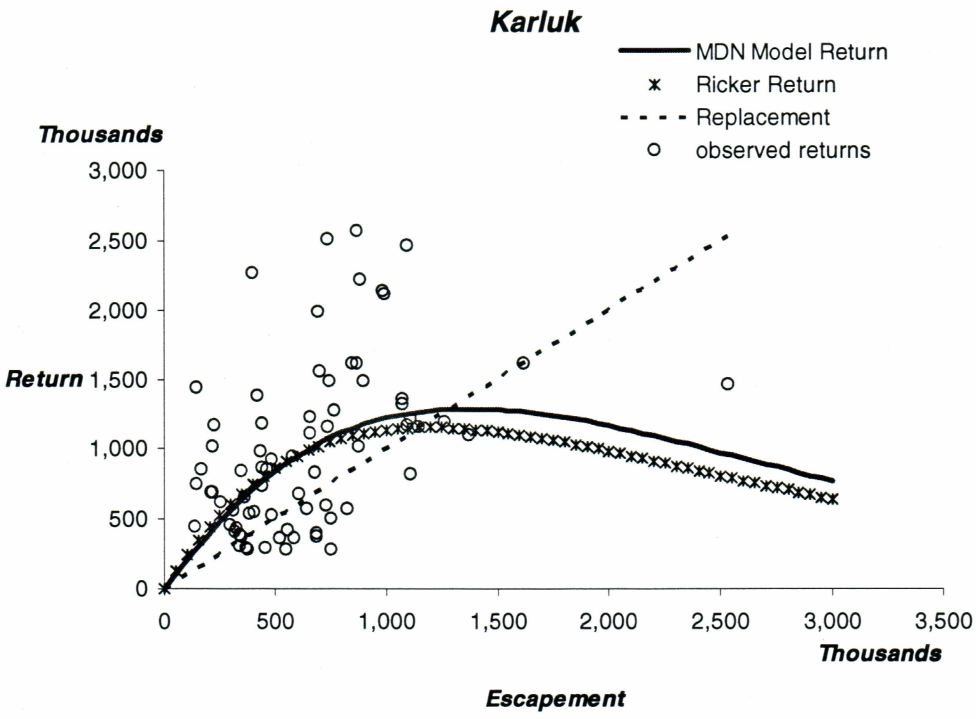

Fig. 3. Simulated stock-recruit relationships for the Karluk stock using the model selected based on AIC_C.

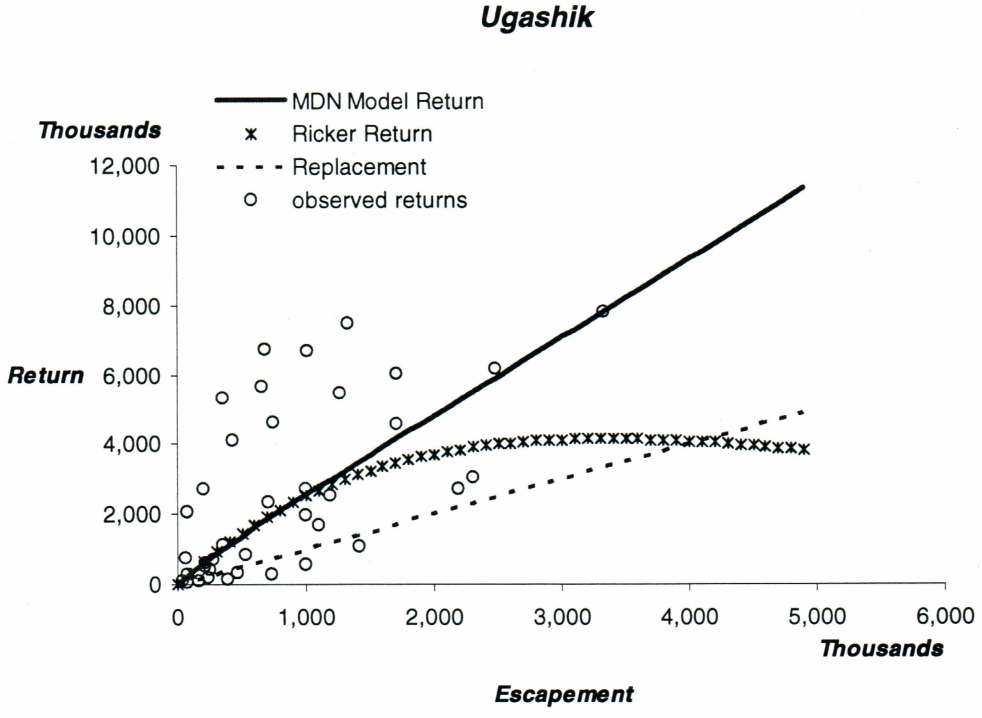

Fig. 4. Simulated stock-recruit relationships for the Ugashik stock using the model selected based on AIC_C.

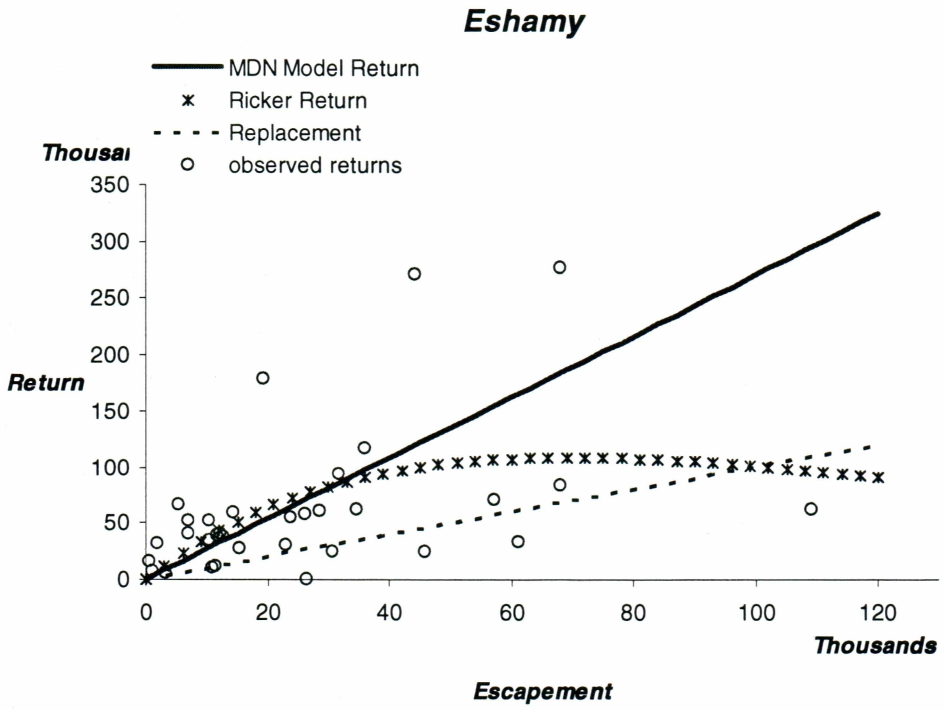

Fig. 5. Simulated stock-recruit relationships for the Eshamy stock using the model selected based on AIC_C.

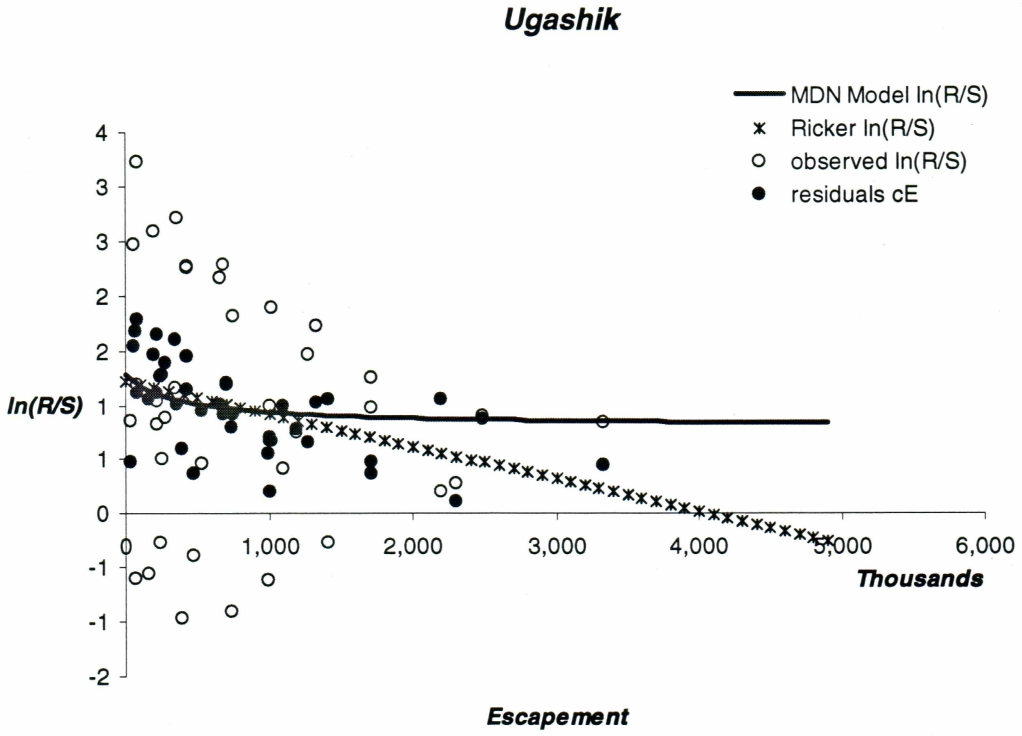

Fig. 6. Simulated ln(R/S) for the Ugashik stock using the model selected based on AIC_C.

Fig. 6 – 8. Simulated ln(R/S) using the model selected based on AIC_C for the Ugashik, Eshamy, and Karluk stocks. The MDN models were run for 100 years at each escapement level using estimated parameters to obtain an equilibrium ln(R/S) (thick solid line). Open circles are observed ln(R/S) for each stock. Closed circles are residuals obtained by subtracting the product of the estimated parameters c_i and $E_{r,t}$ for the MDN models from the observed $\ln(R/S)$.

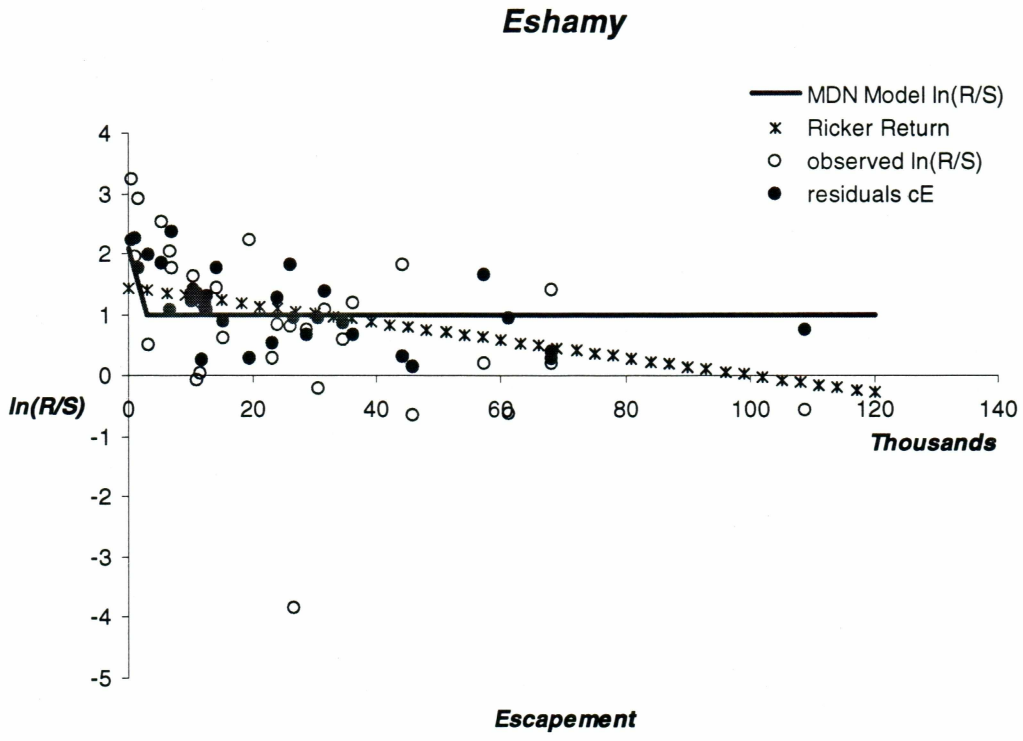

Fig. 7. Simulated ln(R/S) for the Eshamy stock using the model selected based on AIC_C.

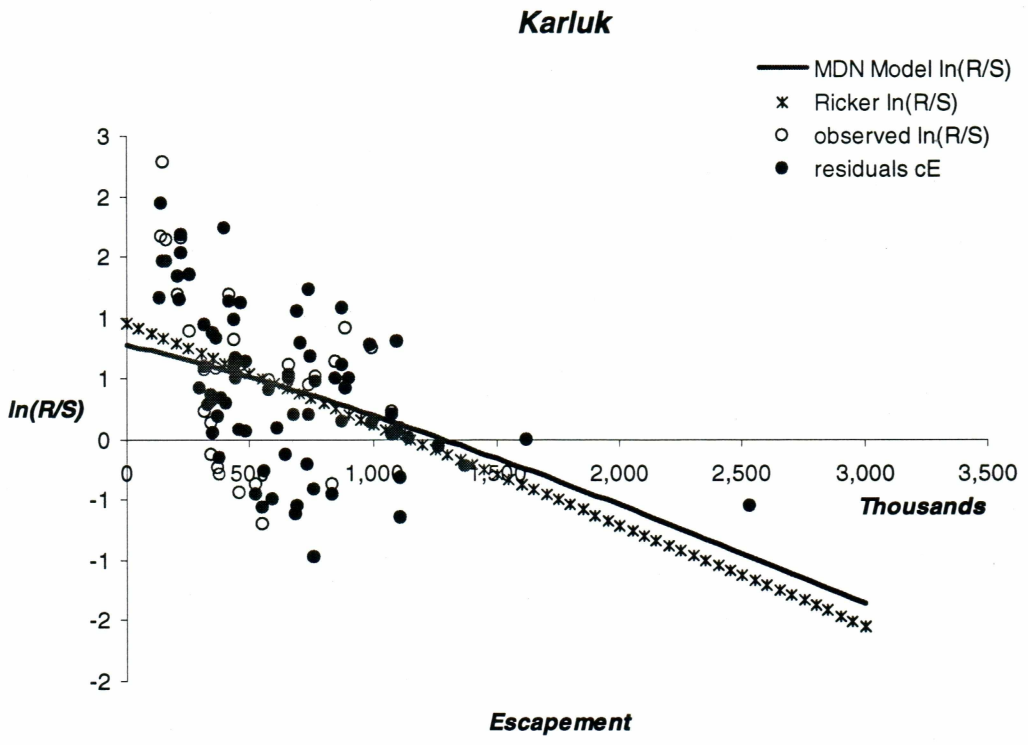

Fig. 8. Simulated ln(R/S) for the Karluk stock using the model selected based on AIC_C.

Table 1. Morphometric and hydrological data for 23 sockeye nursery lakes in Alaska.

Region	Lake	Latitude (°N)	Longitude (°W)	Area (km^2)	Volume ($10^6 m^3$)	Watershed Area (km^2)	Glacier cover (km^2)	Residence Time (year)
Alaska Peninsula	Black	56.46	159.00	41.1	61.65	715.47	9.96	0.058
	Chignik	56.27	158.86	24.1	626.60	1 567.37	36.16	0.270
	Sapsuk	55.68	161.02	11.0	443.1	133.28	0	1.74
Bristol Bay	Becharof	57.95	156.41	1 142.7	64 795	3 375.35	8.74	16.39
	Iliamna	59.55	155.14	2 642.9	115 310	16 862.41	839.38	7.21
	Ugashik (Upper&Lower)	57.5	156.6	381.7	12 188	1 968.84	0	5.78
Kodiak	Akalura	57.19	154.23	4.9	48.0	40.98	0	0.741
	Frazer	57.26	154.14	16.6	551.1	191.70	0	1.82
	Karluk	57.37	154.05	39.4	1920.0	275.08	0	4.64
	Red	57.25	154.30	8.4	207.7	56.31	0	2.35
	Spiridon	57.72	153.69	9.2	319.2	54.18	0	7.97
Cook Inlet	Hidden	60.48	150.25	6.8	138.1	56.17	0	2.83
	Russian, Upper	60.30	149.72	4.6	122.2	66.95	1.500	1.81
	Tustumena	60.19	150.84	294.5	3 6518	1 781.10	382.09	18.85
Prince William Sound	Coghill	61.10	147.82	12.7	381[a]	121.54	22.72	0.90
	Eshamy	60.43	148.17	3.6	122	23.66	0	1.21
Southeast	Auke	58.39	134.63	0.9	17.0	10.16	0	1.09
	Chilkat	59.34	135.91	9.8	319	97.20	3.17	2.03
	Chilkoot	59.36	135.35	7.0	382	333.86	76.67	0.48
	Hugh Smith	55.10	130.67	3.2	192.0[b]	49.41	0	0.94
	McDonald	55.95	131.83	4.2	191.5	120.77	0	0.38
	Redoubt	56.89	135.25	16.6	1 660[c]	108.58	0	4.30
	Speel	58.20	133.56	1.7	5.12	16.51	0	0.075

a. the volume of the lake was adjusted for the depth of a meromictic layer at 30 m.
b. the volume of the lake was adjusted for the depth of a meromictic layer at 60 m.
c. the volume of the lake was adjusted for the depth of a meromictic layer at 100 m.

Table 2. Smolt $\delta^{15}N$ values

Lake	Sample year	Smolt $\delta^{15}N$ (‰)	MDN·lake volume^{-1} ($10^{-6}m^{-3}$)	Watershed (km^2) ·lake volume^{-1} ($10^{-6}m^{-3}$)	Glacier ·watershed^{-1}	Distance from coast (km)	Mixing state
Black	2001	8.63	1.51	11.61	1.39%	47.30	holomictic
	2002	9.34	2.09				
	1999	10.90	179.68				
Chignik	2000	10.80	182.93	2.50	2.31%	7.01	holomictic
	2001	8.99	205.27				
	2002	9.87	288.52				
	1999	8.13	319.52				
Becharof	2000	8.53	326.47	0.05	0.26%	51.40	holomictic
	2001	7.46	322.60				
	1997	8.69	357.00				
Iliamna	1999	9.36	299.75	0.15	4.98%	112.16	holomictic
	2000	9.65	311.10				
	2001	9.01	285.63				
	1999	9.51	528.15				
Ugashik	2000	9.61	569.36	0.16	0%	71.73	holomictic
	2001	9.76	526.97				
Hidden	2004	10.79	914.35	0.41	0%	107.88	holomictic
Tustumena	2004	8.57	111.37	0.05	21.45%	26.75	holomictic
Upper Russian	1995	8.10	1 475.75	0.55	2.24%	147.11	holomictic
Akalura	1997	13.71	113.31	0.85	0%	1.97	holomictic
Frazer	1997	12.60	646.76	0.35	0%	13.70	holomictic
	2001	10.06	623.39				
	1994	12.76	1 832.12				
Karluk	1997	15.74	1 766.66	0.14	0%	41.72	holomictic
	1999	13.97	1 659.24				
	2001	13.21	1 793.13				
Red	1994	16.05	3 970.25	0.27	0%	27.37	holomictic
Spiridon	1997	11.29	0.00	0.17	0%	2.51	holomictic
Coghill	1997	9.06	75.48	0.32	18.69%	5.21	meromictic
Auke	1997	12.57	366.56	0.60	0%	0.78	holomictic
Chilkat	1996	13.00	984.84	0.30	3.26%	31.03	holomictic
	1997	13.40	1 245.00				
Chilkoot	1996	9.47	11.97	0.87	22.96%	1.96	holomictic
Hugh Smith	1996	8.38	30.74	0.26	0%	0.27	meromictic
McDonald	1997	10.99	92.69	0.63	0%	2.01	holomictic
Redoubt	1996	7.72	579.62	0.07	0%	0.00	meromictic
Speel	1996	7.07	1.54	3.23	0%	13.59	holomictic

Table 3. Estimated coefficients, standard errors, and p-values for multiple regression of smolt $\delta^{15}N$.

Coefficient	Estimate	Std. Error	t value	Pr(>|t|)
α (intercept)	8.261	0.983	8.407	1.32e-09
β_1 (MDN)	7.414	1.204	6.157	6.89e-07
β_2 (WS area)	-0.434	0.654	-0.663	0.512
β_3 (glacier)	-0.0225	1.022	-0.022	0.983
β_4 (distance)	-2.409	0.757	-3.181	0.00325
β_5 (mixing)	1.804	0.999	1.804	0.0807

Table 4. Estimated coefficients, standard errors, and p-values for the best multiple regression model of smolt $\delta^{15}N$ based on AIC_C.

Coefficient	Estimate	Std. Error	t value	Pr(>|t|)
α (intercept)	8.228	0.860	9.563	3.61e-11
β_1 (MDN)	7.697	1.054	7.300	1.87e-08
β_4 (distance)	-2.306	0.724	-3.185	0.0031
β_5 (mixing)	1.668	0.923	1.806	0.0797

Table 5. Multiple R^2, residual sum of squares, AIC_C for selected multiple regression models.

Parameters included	Multiple R^2	Adjusted R^2	RSS	AIC_C	Comment
α	0	0	203.55	171.74	Null model
β_1	0.546	0.534	107.53	144.08	MDN input
β_2	0.056	0.029	189.64	171.93	WS area
β_3	0.047	0.020	193.55	172.28	Glacier
β_4	0.058	0.032	190.80	171.83	Distance
β_5	0.030	0.003	193.00	172.95	Mixing
α, β_1, β_4, β_5	0.658	0.627	75.39	138.55	Lowest AIC_C
α, β_1, β_2, β_3, β_4, β_5	0.662	0.610	72.94	143.87	Full model

Table 6. Estimated parameter values of the density-dependent population model without the MDN effect (Ricker model).

Region	Stock	$\overline{\alpha}$	k_α	$\overline{\beta}$	k_β	c	Number of parameters	AICc	% Explained
Alaska Peninsula	Black	4.72	-	596 000	-	-	6	688	47.0%
	Chignik	5.94	-	455 000	-	-			
	Sapsuk	6.41	-	195 000	-	-			
Bristol Bay	Egegik	4.56	-	2.62E+10	-	-	6	540	0.8%
	Kvichak	1.75	-	5.54E+10	-	-			
	Ugashik	3.06	-	5 470 000	-	-			
Kodiak	Frazer	5.49	-	189 000	-	-	6	560	25.1%
	Karluk	2.38	-	1 440 000	-	-			
	Red	2.29	-	2 490 000	-	-			
Cook Inlet and PWS	Coghill	6.03	-	74 400	-	-	6	434	25.6%
	Eshamy	4.31	-	44 100	-	-			
	Kasilof	9.54	-	244 000	-	-			
Southeast	Chilkat	5.89	-	129 000	-	-	8	241	49.9%
	Chilkoot	1.77	-	1.48E+13	-	-			
	Redoubt	5.68	-	25 900	-	-			
	Speel	14.4	-	8 350	-	-			

Table 7. Estimated parameter values of the density-dependent population model without the MDN effect (Ricker model) with the climatic effect.

Region	Stock	$\overline{\alpha}$	k_α	$\overline{\beta}$	k_β	c	Number of parameters	AICc	% Explained
	Black	5.72	-	464 000	-	0.16			
Alaska	Chignik	6.08	-	443 000	-	0.05	83	772	88.3%
Peninsula	Sapsuk	3.67	-	254 000	-	0.18			
	Egegik	4.56	-	2.35E+10	-	0.19			
Bristol	Kvichak	1.75	-	1.11E+11	-	0.17	47	554	68.0%
Bay	Ugashik	3.37	-	3 350 000	-	0.33			
	Frazer	18.1	-	78 700	-	0.66			
Kodiak	Karluk	2.61	-	1 200 000	-	0.18	38	571	60.1%
	Red	4.59	-	333 000	-	0.28			
	Coghill	6.2	-	85 600	-	0.13			
Cook Inlet	Eshamy	4.22	-	69 800	-	0.23	42	496	67.4%
and PWS	Kasilof	9.02	-	265 000	-	0.020			
	Chilkat	5.89	-	129 000	-	4.83E-08			
Southeast	Chilkoot	1.34	-	1.13E+13	-	0.33	30	301	74.5%
	Redoubt	5.68	-	25 900	-	1.24E-06			
	Speel	14.4	-	8 350	-	2.13E-09			

Table 8. Estimated parameter values of the population model that includes the MDN effect on both productivity (α) and carrying capacity (β) without the climatic effect.

Region	Stock	$\overline{\alpha}$	k_α	$\overline{\beta}$	k_β	c	Number of parameters	AICc	% Explained
Alaska Peninsula	Black	5.16	1.23E-16	496 000	284	-	12	699	47.8%
	Chignik	4.57	2.76E-05	340 000	2.60E-08	-			
	Sapsuk	6.41	7.09E-14	195 000	9.63E-06	-			
Bristol Bay	Egegik	4.56	2.80E-11	2.62E+10	1.11E-09	-	12	555	0.8%
	Kvichak	1.75	2.11E-13	5.54E+10	16.6	-			
	Ugashik	3.06	2.23E-14	5 470 000	2.89E-09	-			
Kodiak	Frazer	5.49	1.00E-10	189 000	1.00E-13	-	12	573	25.8%
	Karluk	1.98	2.74E-07	1 070 000	1.00E-08	-			
	Red	2.29	9.99E-13	2 490 000	9.98E-07	-			
Cook Inlet and PWS	Coghill	8.17	3.08E-11	34 300	0.270	-	12	447	26.8%
	Eshamy	4.31	7.74E-10	44 100	5.31E-08	-			
	Kasilof	9.54	1.17E-11	244 000	1.50E-11	-			
Southeast	Chilkat	7.19	4.06E-11	51 600	0.260	-	16	246	63.9%
	Chilkoot	2.85E-09	5.79E-05	1.13E+13	23 434	-			
	Redoubt	5.73	1.77E-15	22 300	0.00490	-			
	Speel	102	5.32E-08	1 040	114	-			

Table 9. Estimated parameter values of the population model that includes the MDN effect on both productivity (α) and carrying capacity (β) with the climatic effect.

Region	Stock	$\overline{\alpha}$	k_α	$\overline{\beta}$	k_β	c	Number of parameters	AICc	% Explained
Alaska Peninsula	Black	30.6	1.82E-08	31 400	1 601	0.15	89	800	90.1%
	Chignik	6.79	1.06E-18	270 000	0.800	0.07			
	Sapsuk	1.01	7.09E-14	458 000	9.63E-06	0.41			
Bristol Bay	Egegik	4.56	2.80E-11	2.62E+10	1.11E-09	0.18	53	591	68.3%
	Kvichak	1.75	2.11E-13	5.54E+10	16.6	0.16			
	Ugashik	3.59	2.23E-14	810 000	0.370	0.31			
Kodiak	Frazer	18.09	1.00E-10	78 700	1.00E-13	0.66	44	593	60.8%
	Karluk	2.18	2.96E-07	938 000	1.00E-08	0.18			
	Red	4.57	9.99E-13	334 000	9.98E-07	0.28			
Cook Inlet and PWS	Coghill	7.43	3.08E-11	48 200	0.250	0.10	48	538	68.3%
	Eshamy	8.95	8.03E-10	3.29E-07	0.690	0.27			
	Kasilof	9.28	2.92E-11	254 000	1.55E-06	0.01			
Southeast	Chilkat	7.19	4.06E-11	51 600	0.260	2.22E-16	38	346	86.5%
	Chilkoot	1.92E-10	4.42E-05	1.13E+13	434	0.24			
	Redoubt	5.73	1.77E-15	22 300	0.00490	5.28E-10			
	Speel	138	5.32E-08	828	116	0.05			

Table 10. Proportions of the intrinsic productivity (I_α) and carrying capacity (I_β) attributed to MDN based on estimated parameters. In comparison to the baseline productivity ($\overline{\alpha}$) and carrying capacity ($\overline{\beta}$). The values less than 0.001 were left blank.

Region	Lake	I_α	I_β
AKP	Black	-	0.73
	Chignik	-	0.26
	Sapsuk	-	-
BB	Egegik	-	-
	Kvichak	-	0.01
	Ugashik	-	0.66
KOD	Frazer	-	-
	Karluk	0.28	-
	Red	-	-
CI.PWS	Coghill	-	0.18
	Eshamy	-	> 0.99
	Kasilof	-	-
SE	Chilkat	-	0.51
	Chilkoot	> 0.99	-
	Redoubt	-	0.11
	Speel	-	0.64

Table 11. Estimated parameter values of the best models with a climatic effect. Models ranked first or second based on the AICc are shown for each stock.

Region	Stock	$\overline{\alpha}$	Kα	$\overline{\beta}$	Kβ	c	# par	AICc	% Explained
AKP	Black	30.69	-	5.86E+04	1 171	0.76	84	761	89.6%
	Chignik	5.43	-	5.07E+05	-	0.28			
	Sapsuk	2.44	-	2.79E+05	-	0.85			
	Black	30.65	1.82E-08	5.87E+04	1 170	0.22	85	770	89.6%
	Chignik	5.43	-	5.06E+05	-	0.08			
	Sapsuk	2.44	-	2.79E+05	-	0.25			
BB	Egegik	4.56	-	2.35E+10	-	0.19	47	554	68.0%
	Kvichak	1.75	-	1.11E+11	-	0.17			
	Ugashik	3.37	-	3.35E+06	-	0.33			
	Egegik	4.56	-	2.57E+10	-	0.25	48	559	68.3%
	Kvichak	1.75	-	5.84E+15	-	0.23			
	Ugashik	3.59	-	8.11E+05	0.366	0.44			
KOD	Frazer	18.07	-	7.87E+04	-	0.66	38	571	60.1%
	Karluk	2.61	-	1.20E+06	-	0.66			
	Red	4.59	-	3.33E+05	-	0.66			
	Frazer	18.10	-	7.86E+04	-	0.66	39	572	60.8%
	Karluk	2.18	2.96E-07	9.38E+05	-	0.18			
	Red	4.57	-	3.34E+05	-	0.28			
CI.PWS	Coghill	6.20	-	8.56E+04	-	0.13	42	496	67.4%
	Eshamy	4.22	-	6.98E+04	-	0.23			
	Kasilof	9.02	-	2.65E+05	-	0.02			
	Coghill	6.37	-	8.35E+04	-	0.03	43	501	67.9%
	Eshamy	8.04	-	3.29E-07	0.78	0.08			
	Kasilof	9.12	-	2.60E+05	-	0.01			
SE	Chilkat	5.89	-	1.29E+05	-	4.83E-08	31	272	86.0%
	Chilkoot	1.34	-	1.13E+13	-	0.33			
	Redoubt	5.68	-	2.59E+04	-	1.24E-06			
	Speel	102.28	-	1.04E+03	114	2.13E-09			
	Chilkat	5.89	-	1.29E+05	-	4.83E-08	32	280	86.0%
	Chilkoot	1.34	-	1.13E+13	-	0.33			
	Redoubt	5.68	-	2.59E+04	-	1.24E-06			
	Speel	102.28	5.32E-08	1.04E+03	114	2.13E-09			

Table 12. MSY, S_{MSY} and carrying capacity (β) for the equilibrium stock-recruit relationship.

stock	model	MSY	S_{MSY}	Max. return	β
Black	k_β	765 934	90 259	866 601	113 842
	cE	599 844	307 022	977 275	464 168
Ugashik	k_β	-	-	-	-
	cE	1 748 139	1 699 476	4 153 167	3 351 644
Karluk	k_α	348 660	601 642	1 288 198	1 372 307
	cE	359 980	501 046	1 150 882	1 198 440
Eshamy	k_β	-	-	-	-
	cE	55 129	40 328	108 332	69 829
Speel	k_β	45 509	1 491	47 038	1 568
	cE	36 467	7 002	44 107	8 347

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General Conclusions

This study showed that the nutrients released from carcasses of adult salmon are incorporated into the lentic ecosystem of sockeye nursery lakes and make an important contribution to the nutrition of juvenile salmon. Lake and watershed characteristics found to be important in the transfer of nutrients from carcasses of adult salmon to sockeye smolts were water residence time, distance from the coast, and whether the water column mixes. Conditions under which salmon fry benefit most from MDN input from spawning sockeye are lakes with long water residence times, short distances from the coast, and the water columns that undergo complete mixing annually.

Although there was strong evidence for the influences of MDN on sockeye smolt, and strong evidence that hydrological characteristics of nursery lakes affect the strength of this effect, the analyses of sockeye stock-recruitment relationships did not provide much evidence to support the hypothesis that increases in MDN input to sockeye nursery lakes result in increased productivity of sockeye stocks. Environmental conditions were found to have a much larger influence on sockeye stock productivity than that of MDN by the model analysis. However, stock-recruitment data may be poorly suited to detecting the influence of MDN on productivity.

A more direct investigation of the mechanisms by which MDN might improve stock productivity (growth, age at seaward migration, total biomass of smolt produced, and subsequent marine survival) would help improve our understanding of the effects of MDN on productivity. Further investigations on how MDN are transferred, recycled, and retained in the limnetic ecosystem would also be helpful for future modeling efforts.

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